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THE MANDIBULAR DENTITION OF *PLAGIOMENE* (DERMOPTERA, PLAGIOMENIDAE)

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ABSTRACT. The peculiar bilobate lower incisors and the anterior lower premolars of the Early Eocene genus *Plagiomene* are described for the first time. Several groups of mammals have independently acquired incisors with divided crowns, but available evidence suggests that any resemblances to *Plagiomene*, except in the case of Recent dermopterans, can be attributed to convergence. Nevertheless, the close resemblance between the incisors of *Plagiomene* and those of certain Recent elephant shrews (Macroscelididae) may be indicative of similar incisor function. The hypothesis that Recent dermopterans (Galeopithecidae) are descended from *Plagiomene* or a closely allied form (a view previously based primarily on molar morphology) is strengthened by the specimens described here. A brief review of fossil forms that have been referred to the Dermoptera is presented, and it is concluded that, at present, only two fossil genera, *Plagiomene* and *Planetetherium*, can with reasonable probability be assigned to the Dermoptera.

INTRODUCTION

The Early Eocene genus *Plagiomene* has been widely regarded as an early member of the Dermoptera, a view based on the molar morphology, which is similar to that in living dermopterans. Fossil evidence of dermopteran evolution is extremely scarce. Although *Plagiomene* is better known than any other fossil forms that may be considered Dermoptera, it is represented only by dental and gnathic remains. Previous literature on fossil dermopterans (known forms of which are all assigned to the family Plagiomenidae) is minimal, and has been

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restricted to descriptions of parts of the dentition. None of the anterior dentition has been described or adequately figured before, although the unusual incisors have been noted previously (Jepsen, 1962, 1970; Van Houten, 1945). The nearly complete lower dentition of *Plagiomene* described here (PU 14551, right mandible, and PU 14552, associated left mandible) is significant in providing new evidence that *Plagiomene* is related to and possibly ancestral to extant dermopterans. In addition, an incomplete right mandible, PU 13268, provides the first knowledge of the deciduous premolars in *Plagiomene*.

Comparative material of *Plagiomene* and other forms has been examined during this study. Abbreviations used in the text are as follows:

- AMNH American Museum of Natural History, New York
- MCZ Museum of Comparative Zoology (Mammalogy Collection), Harvard University, Cambridge, Massachusetts
- PU Princeton University Museum, Princeton, New Jersey
- YPM Peabody Museum of Natural History, Yale University, New Haven, Connecticut

DESCRIPTION

The lower dental formula of *Plagiomene*, 3.1.4.3, deduced by Matthew (1918) from fragmentary specimens, is confirmed by PU nos. 14551 and 14552 (see Fig. 1).

The three lower incisors (Figs. 1, 2, 4) of *Plagiomene* are semiprocumbent, with broad, bilobate crowns, of which the mesial lobe is the larger. Faint longitudinal depressions on the lingual sides of these larger lobes in I_1 and I_2 (see Fig. 1 lower) are potential sites for further digitation of the incisor crowns. The crowns are slightly convex on the buccal surface and somewhat concave lingually. The incisors diminish in size from I_1 to I_3 , I_1 being considerably larger than I_3 . They have an oval, mesiodistally compressed cross section at the root. In the absence of the crowns, Matthew (1918) inferred from the roots that the incisors were small and unspecialized. The specimens discussed here show this inference to have been incorrect. Expansion of the incisors (mostly mesiodistally) occurs at the base of the crowns and increases towards the tip. There are no cingula. A small wear facet on the labiodistal surface of the mesial lobe of left I_1 suggests that upper incisors may have occluded with the lower incisors. This is of interest because in the Recent forms, in

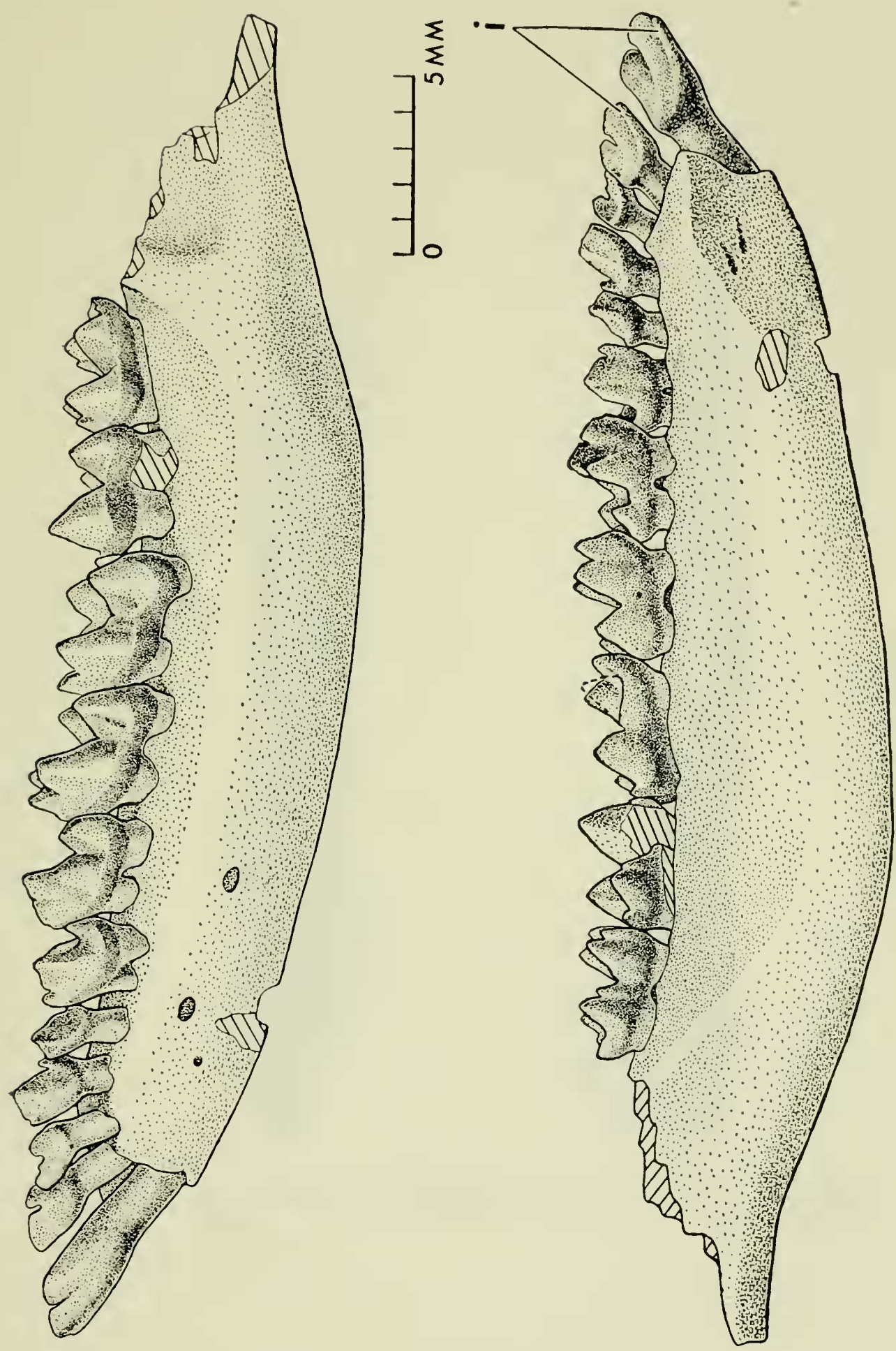


Figure 1. (Upper) *Plagiomene multicuspis* Matthew. Left mandible, PU 14552, lateral view.
(Lower) Medial view of same; *i* designates incipient third lobe of I_1 and I_2 .

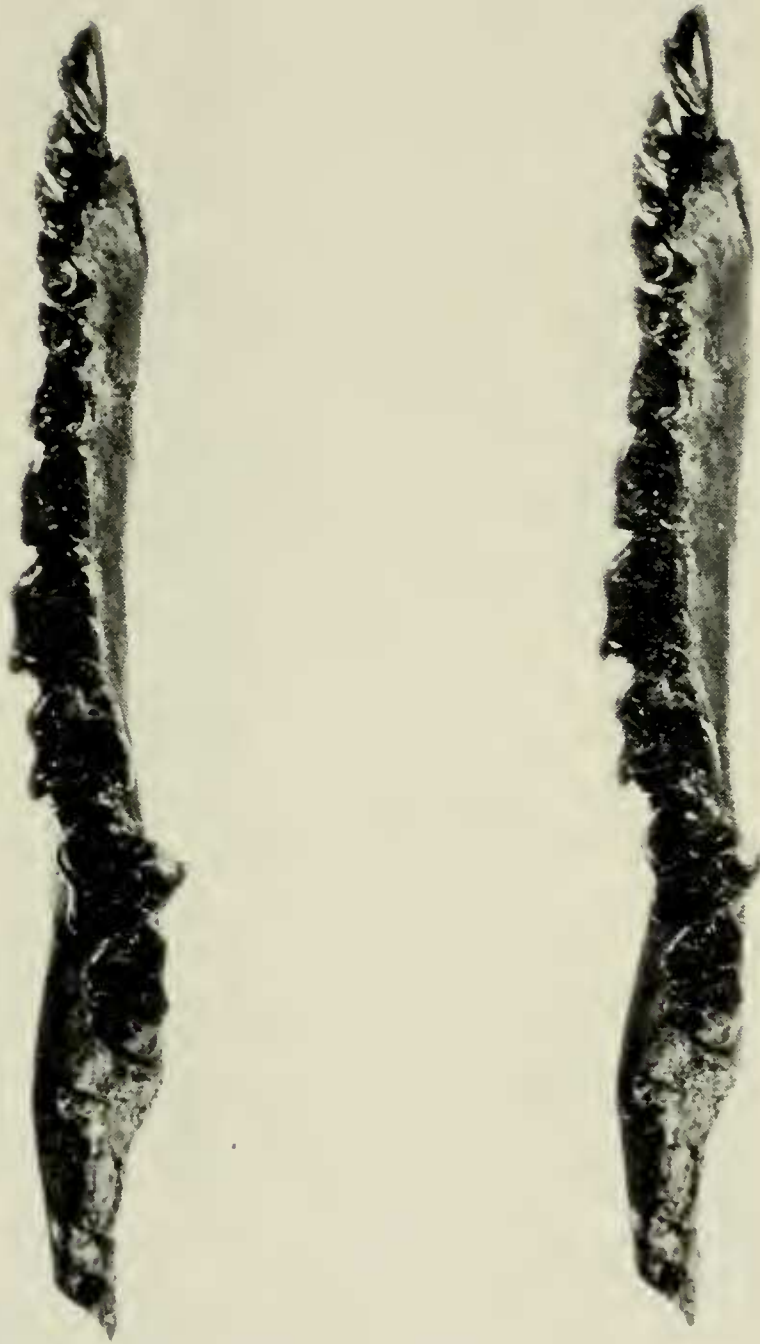


Figure 2. Occlusal view of left mandibular dentition, PU 14552.

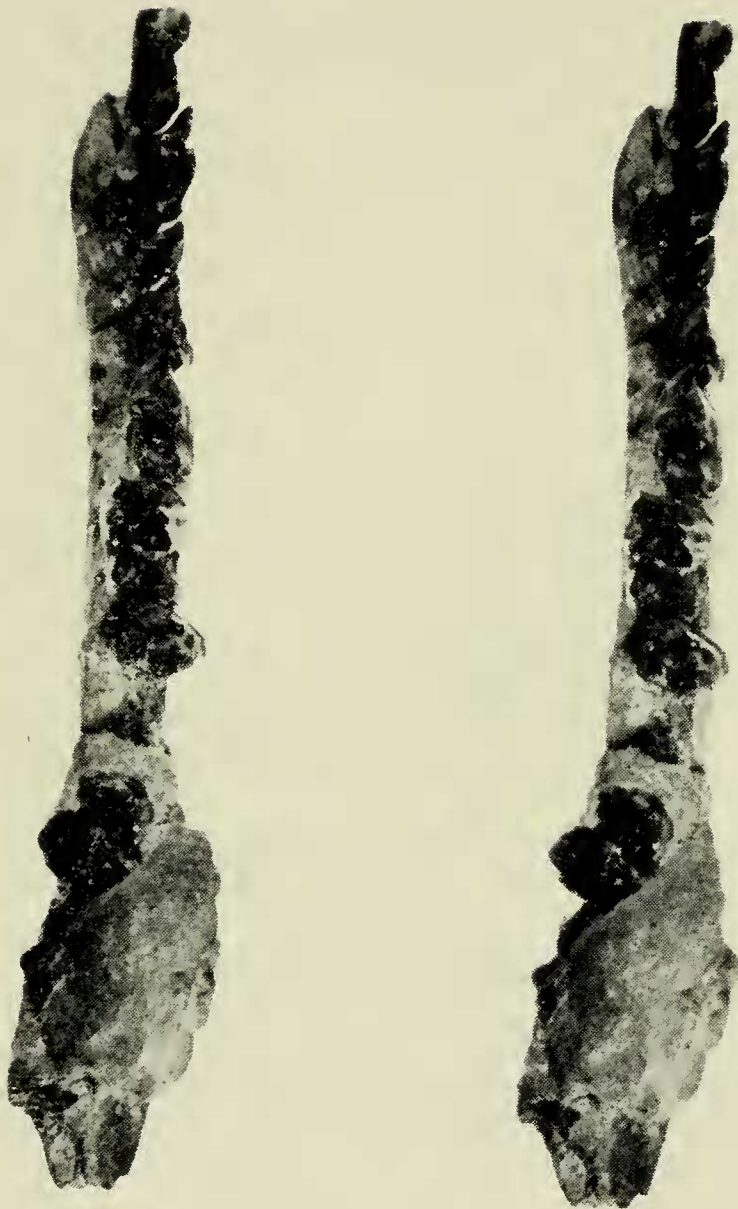


Figure 3. Occlusal view of right mandibular dentition, PU 14551.

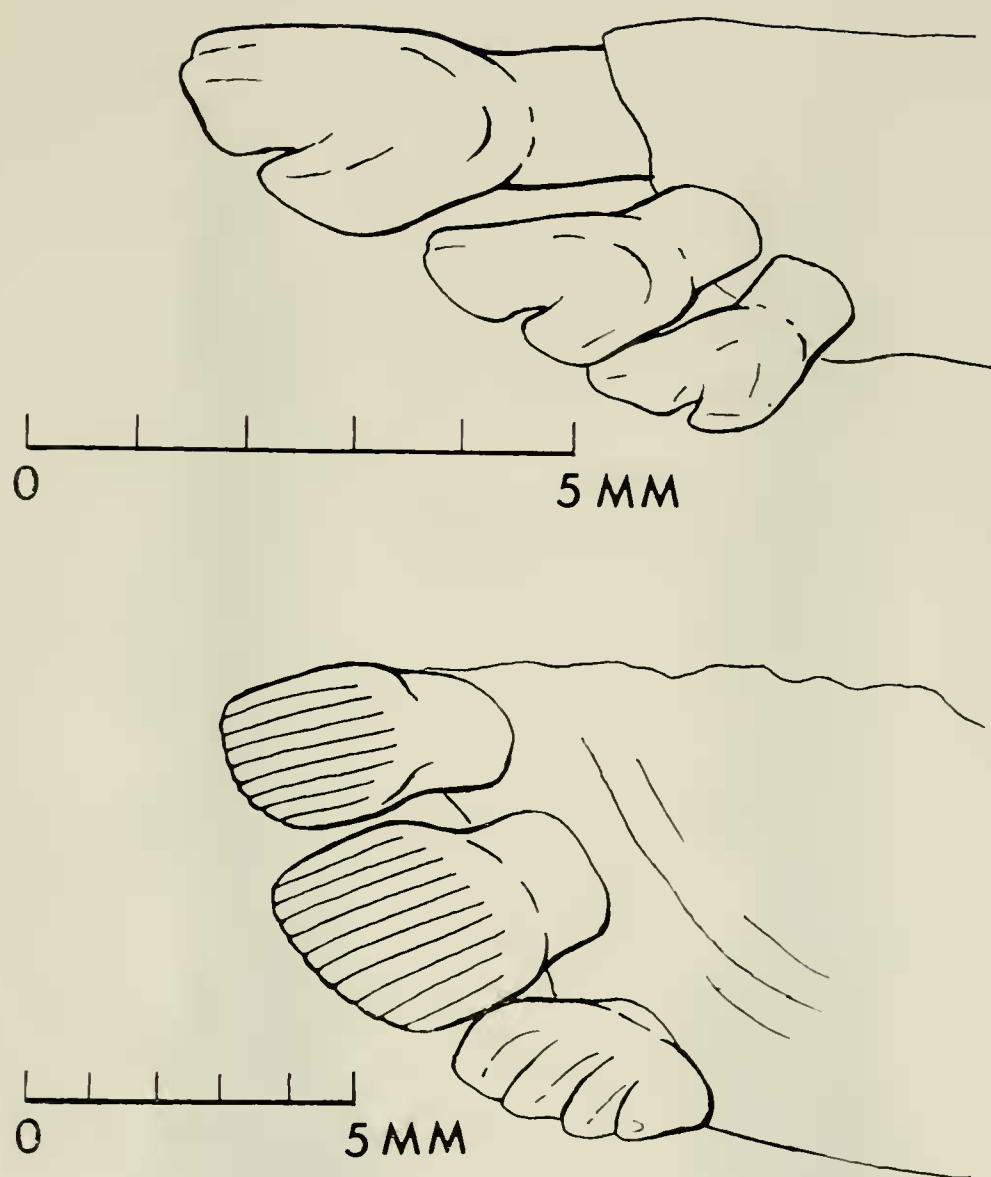


Figure 4. Comparison of lower left incisors (I₁ at top) of *Plagiomene* (above) and *Cynocephalus* (below).

TABLE I
MEASUREMENTS (in mm) OF MANDIBULAR TEETH
OF *PLAGIOMENE*

| | | PU 14552 | PU 13268 (Deciduous teeth) |
|----------------|---|----------|-------------------------------|
| I ₁ | maximum mesiodistal length | 2.3 | |
| | maximum height of crown (measured lingually) | 3.4 | |
| I ₂ | maximum mesiodistal length | 2.0 | |
| | maximum height of crown (measured lingually) | 2.5 | |
| I ₃ | maximum mesiodistal length | 1.4 | |
| | maximum height of crown (measured lingually) | 1.8 | |
| C | maximum length | 2.0 | |
| | maximum breadth | 1.4 | |
| P ₁ | maximum length | 1.7 | |
| | maximum breadth | 1.3 | |
| P ₂ | maximum length | 2.8 | 2.3 (dP ₂) |
| | maximum breadth | 2.0 | 1.2 (dP ₂) |
| P ₃ | maximum length | 3.7 | 3.5 (dP ₃) |
| | maximum breadth | 2.3 | 2.0 (dP ₃) |
| P ₄ | maximum length | 4.3 | 4.3 (dP ₄) |
| | maximum breadth, trigonid | 2.8 | 1.9 (dP ₄) |
| | maximum breadth, talonid | 3.2 | 2.3 (dP ₄) |
| M ₁ | maximum length | 4.3 | |
| | maximum breadth, trigonid | 3.0 | |
| | maximum breadth, talonid | 3.5 | |
| M ₂ | maximum length | 4.0 | |
| | maximum breadth, trigonid | 3.1a | |
| | maximum breadth, talonid | 3.3a | |
| M ₃ | maximum length | 3.9 | |
| | maximum breadth, trigonid | 2.4 | |
| | maximum breadth, talonid | 2.4 | |

a, = approximate (tooth damaged)

which I¹ is lost and I² is reduced, the anteriormost upper teeth have migrated distally, so that the lower, comblike incisors meet an edentulous area during centric occlusion. The most complete upper dentition known for *Plagiomene*, AMNH 15208 (Szalay, 1969: 241), shows diminishing tooth size anteriorly, however, and does not preserve any incisors (except possibly

I³). This may indicate reduction or loss of the anterior upper teeth as in extant dermopterans.

The single-rooted lower canine (Fig. 1) of *Plagiomene* is premolariform, consisting of a large anterior cusp, which rises above the crowns of the incisors and of P₁, and a prominent but low heel. A low, incipient cusp is observed on the anterior border. The canine is laterally compressed and its root is elliptical in cross section.

The first premolar is a small, single-rooted tooth bearing one major cusp that may be followed by a much lower, small cuspule. Behind this is a still lower, incipient talonid cusp.

P₂ (Figs. 1–3), a much larger tooth than P₁, is double-rooted and “premolariform-semimolariform” (as defined by Szalay, 1969: 199). The prominent protoconid is preceded by a distinct though much smaller and lower paraconid, which is situated directly anterior to the protoconid (not anterolingual to it, as in the teeth behind P₂). The talonid is much broader and longer than in P₁, but still consists of only a single distinct cusp, homologous to the hypoconid.

The third premolar is semimolariform. The protoconid is the largest cusp, and there is a conspicuous, lower paraconid anterolingual to it. A less prominent metaconid develops from the posterolingual border of the protoconid. Some individuals (*e.g.*, YPM nos. 24966 and 24971) have a small, lower cuspule anterior to the paraconid. The trigonid is somewhat extended anteroposteriorly and there is no trigonid basin. The talonid is well developed, with both hypoconid and entoconid prominent, and with a rudimentary hypoconulid. The talonid basin is closed posteriorly but is open anteriorly in a deep buccolingual valley separating the trigonid and the talonid. This feature is more strongly expressed in the molariform teeth.

P₄ is fully molariform, differing from M₁ chiefly in its slightly smaller size, but these two teeth are frequently almost indistinguishable. The three trigonid cusps and two main talonid cusps of P₄ are large and sharp; the hypoconulid is lower and smaller. Some specimens (*e.g.*, YPM 23578) have a small entoconulid anterior to the entoconid.

The lower molars have been previously figured and described (Matthew, 1918), but a few features may be noted. M_{1–3} are very similar to each other. The trigonid cusps are high and sharp; the metaconid is usually as high as the protoconid or higher, and the paraconid is somewhat lower. In the talonid a

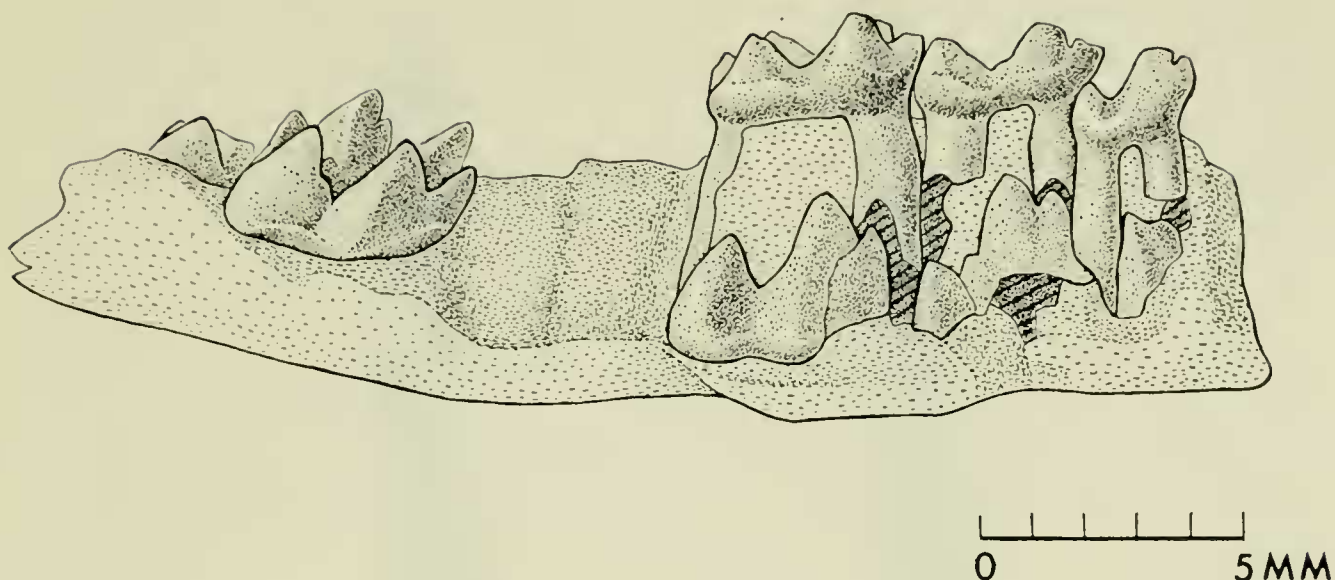


Figure 5. Right mandible with functional deciduous premolars (dP_{2-4}) and unerupted permanent P_{2-4} ; M_2 is in process of eruption. Lateral view of PU 13268.

pronounced entoconulid is anterior to the entoconid on M_2 and M_3 , and it is present on M_1 in some individuals. Posterior to the hypoconulid, the postcingulid rises in a broad cusplike projection. This is well developed in M_1 and M_2 and, to a lesser extent, in P_4 . In M_3 the hypoconulid forms a small third lobe. M_3 is usually narrower buccolingually than the other molars. The enamel of the molariform teeth is moderately crenulated, particularly in the talonid. A prominent ectocingulid is present on P_3 – M_3 and posteriorly on P_2 . The posterior premolars and the molars clearly demonstrate a tendency toward polycuspida-tion, a characteristic of the Plagiomenidae.

The deciduous premolars preserved in PU 13268, dP_{2-4} (see Figs. 5 and 6), are in general similar to their adult replacements. They possess the same cusps in approximately the same positions but are relatively longer anteroposteriorly and more compressed buccolingually. The talonid of dP_2 is more molariform than in P_2 , exhibiting both a hypoconid and a small entoconid. The talonid of dP_3 is similarly more expanded than that of the replacing tooth. In the trigonid of dP_3 the paraconid and metaconid are somewhat more distinct and better separated from the protoconid than in the permanent P_3 . In dP_4 as well, the talonid is elongated and expanded relative to its condition in P_4 , and the hypoconulid is much more pronounced, almost forming a small third lobe as in M_3 .

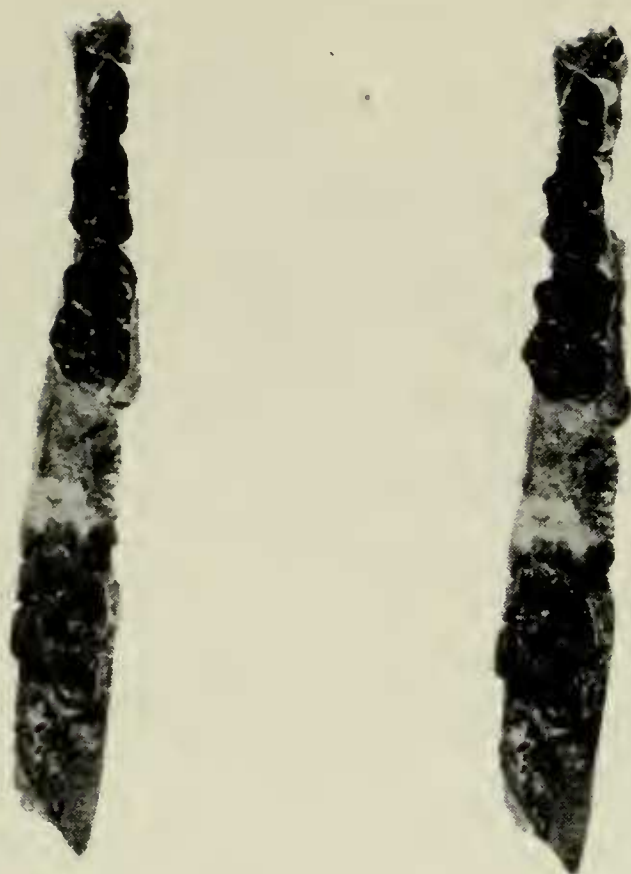


Figure 6. Occlusal view of PU 13268.

DISCUSSION

Incisor specializations comparable to those occurring in *Plagiomene* are found in several other mammals. Incisors with digitate crowns have evolved independently in several unrelated groups, including Carnivora, Notoungulata, Macroscelidea, Dermoptera, and Insectivora. Among these, carnivores such as *Canis* and *Ursus* show tendencies toward digitation of the incisor crowns, but to a less marked degree than in *Plagiomene*, and there is surely no relationship involved. Patterson (1940) described the deciduous incisors of the notoungulate "*Progaleopithecus*" (= *Archaeophylus*), so-named by Ameghino in reference to the dermopteran-like, pectinate incisor crowns, but there is no reason to believe that *Plagiomene* is in any way related to the Notoungulata.

Among the Insectivora, *Nesophontes*, a recently extinct Antillean form (McDowell, 1958: fig. 3), possesses bilobate incisors very similar to those in *Plagiomene*. *Tenrec* also shows a slight tendency toward digitation of the incisor crowns. There is little resemblance of the lower cheek teeth or the upper dentition of these forms to *Plagiomene*, however. The superficial similarities again may be attributed to convergence.

Certain Recent elephant shrews (Macroscelididae) bear a remarkable likeness to *Plagiomene* in the conformation of the incisors; the most striking examples are *Petrodromus* and particularly *Rhynchocyon*. In the former, the crowns of the permanent incisors are bilobate, while the milk incisors (e.g., MCZ 26113) may have three or four lobes. The lower incisors of *Rhynchocyon* are the closest to *Plagiomene* of any forms examined. They are, however, all approximately of equal size in *Rhynchocyon*, in contrast to the decrease in size from I_1 to I_3 in *Plagiomene*. The remainder of the macroscelidid dentition is quite unlike that of *Plagiomene*. The most obvious contrasts are the loss of M_3^3 (in the majority of known macroscelidids, including both genera mentioned here) and the peculiar structure of the molariform teeth (P_4^4 , M_1^1 , M_2^2). Macroscelidids are not common in the fossil record, and of those known (Patterson, 1965; Butler and Hopwood, 1957), none show any particular resemblance to *Plagiomene*. The family is unknown outside Africa. Therefore, the similar form of the incisors in some Recent macroscelidids is surely not indicative of any close relationship, although it may reflect functional similarities.

Matthew (1918: 599) noted that the molars of the talpid *Myogale* (= *Desmana*) were of somewhat similar structure to those of *Plagiomene*. Although he viewed this as "perhaps significant of a real though remote affinity" (*ibid.*: 600), the resemblances do not extend to the other teeth. It is unlikely that *Plagiomene* is related to talpids.

Plagiomene has most frequently been compared with the living dermopterans, Galeopithecidae (e.g., Matthew, 1918; Romer, 1966; Szalay, 1969; Jepsen, 1970; among others), and alliance with this group still appears to be the most likely possibility. Matthew (1918) first suggested a relationship between the two groups after studying the molars of *Plagiomene*, which he described as "unlike any placental molars known to me except those of *Galeopithecus*" (*ibid.*: 601). Indeed, the molariform teeth (P_4^4 – M_3^3 , as in *Plagiomene*) of extant dermopterans show many features in common with *Plagiomene*: prominent conules; absence of hypocone; paracone and metacone situated well lingual to the buccal margin; low paraconid; presence of an entoconulid; talonid and trigonid separated by a deep buccolingual valley; and crenulated enamel. Furthermore, P_4^4 and, to a lesser extent, P_3^3 are molarized as in *Plagiomene*. Although

the lower incisors of galeopithecids exhibit less resemblance to those of *Plagiomene* than do most of the forms discussed above, the long time interval separating these two forms must be taken into account. It seems highly probable that the comblike incisors of galeopithecids must ultimately have been derived from incisors with divided crowns such as those present in *Plagiomene* (see Fig. 4). In fact, the form of I_3 in extant dermopterans is an approximate morphologic intermediate between the form of the incisors in *Plagiomene* and the pectinate condition of I_1 and I_2 in the living forms. The dental formula of the Galeopithecidae differs from that of *Plagiomene*, in the loss of two antemolar teeth (probably P_1 and P_2); this is easily explained, however, for the reduction or loss of teeth is common in species that evolve enlarged, specialized teeth, such as the pectinate incisors of galeopithecids. In summary, the new evidence provided by the anterior dentition of *Plagiomene* strengthens the view that it is in or near the ancestry of the Recent Dermoptera.

This view, however, has been questioned recently. Van Valen (1967) regarded the Dermoptera as a suborder of the Insectivora. He suggested (*ibid.*: 271) that the Galeopithecidae may have been derived from *Adapisoriculus* (or an unknown related form) rather than from the Plagiomenidae, which he considered to be "unrelated to the Galeopithecidae" (although including both Plagiomenidae and Galeopithecidae in the same superfamily of the Dermoptera, and placing *Adapisoriculus* in a suborder separate from the Dermoptera).

From the preceding discussion, it is clear that incisors with divided crowns have arisen independently in many unrelated mammals and that such incisors function in various ways. Although incisors of different general morphology are included in this discussion, some of those mentioned above exhibit close resemblances to those of *Plagiomene*. Based on these similarities, incisor function in *Plagiomene* may have been close to that in *Nesophontes*, *Petrodromus*, and *Rhynchocyon*, and probably not so much like that in extant dermopterans. Unfortunately, little is known of incisor use in any of these forms. Flying lemurs are reported to use their comblike incisors "in scraping the green coloring out of leaves" (Gregory, 1951: 387, quoting H. C. Raven), in ingesting leaves (Winge, 1941), or in grooming (Wharton, 1950). They are strictly herbivorous, feeding mainly on leaves, but including shoots, buds, soft fruit, and coconut blossoms in their diet (Wharton, 1950; Walker et al.,

1964; Medway, 1969). In contrast, macroscelidids are primarily insectivorous, feeding largely on ants (Brown, 1964), but almost nothing is known of how macroscelidids use their incisors.

Hiiemäe and Kay (1973) stress that incisors frequently function in processes other than food ingestion and, in fact, that minimal use of incisors during ingestion in primitive mammals provided the opportunity to develop incisor specializations unrelated to feeding. Therefore, it may not be correct to speculate that the diet of *Plagiomene* was similar to that of macroscelidids (indeed, differences in premolar and molar morphology would seem to be against such a supposition); but it does seem likely that in both there are similarities of incisor function.

Fossil forms that have been assigned to the Dermoptera are rare and are represented solely by jaws and teeth. Only two monotypic genera, *Plagiomene* (from the Early Eocene of Wyoming) and *Planetetherium*¹ (from the latest Paleocene of Montana), can with reasonable assurance be referred to the family Plagiomenidae, the only known family (in addition to the Recent Galeopithecidae) referred to the order. *Planetetherium* (Simpson, 1928, 1929; Szalay, 1969) is almost certainly the direct ancestor of *Plagiomene*. It is known from only one locality, the Eagle Coal Mine at Bear Creek, Montana, where it occurs in carbonaceous shale just above the coal layer (Van Valen and Sloan, 1966). The site evidently represents an ancient swamp, and many of the mammals present (including *Planetetherium*) were probably arboreal (Simpson, 1928; Van

¹Grassé (1955: 1727, fig. 1698) reproduced drawings of isolated incisors, from Simpson (1928: figs. 12 and 13), and attributed the incisors to *Planetetherium*. This is apparently an unintentional error, which may have occurred because the description of the incisors (which Simpson, p. 14, stated "cannot be definitely classified or correlated with cheek teeth as yet") immediately followed the discussion of *Planetetherium* in Simpson's paper. Simpson believed that the incisors in question belonged to insectivores or primates, but he suggested no association with *Planetetherium*. The morphologies observed differ substantially, indicating that more than one taxon is involved. Inasmuch as *Planetetherium* is the most abundant form at Bear Creek, it seems not improbable that it is among the forms represented by the incisors. Szalay (1972: 25, figs. 1-9) has recently referred one of these incisors, AMNH 22153, to the primate *Carpolestes*, a common occurrence at Bear Creek. There is little evidence to confirm this allocation and, in fact, the morphology of AMNH 22153 may be closer to what might be expected in *Planetetherium* than in *Carpolestes*.

Valen and Sloan, 1966; Jepsen, 1970). *Planetetherium* is by far the most commonly found member of the Bear Creek fauna.

Several isolated teeth from the Early Eocene of France are the basis for a new genus and species being described by D. E. Russell, P. Louis, and D. E. Savage (in press) and regarded by them as a plagiomenid dermopter. Casts of the teeth show features that suggest to me, however, that the new form may be neither a plagiomenid nor even a dermopter. More complete evidence may in the future substantiate allocation of this form to the Plagiomenidae, but I do not believe that presently available evidence is sufficiently convincing for such an assignment.

L. S. Russell (1954) proposed *Thylacaelurus montanus* based on a maxillary fragment from the Kishenehn Formation (Late Eocene ?), British Columbia, which he believed to have marsupial affinities. Although the specimen probably represents a placental (McKenna, in Van Valen, 1965: 394), Van Valen's (1967) allocation of the genus to the Plagiomenidae is unjustified (see also Szalay, 1969: 242). Its relationships will remain obscure until further material is available.

Van Valen (1967) referred the Mixodectidae to the Dermoptera. This move also seems unwarranted, but the resemblance of *Elpidophorus* to the plagiomenids may be significant. This comparison is not new. Simpson (1936) first discussed this similarity and suggested that *Elpidophorus* provided a suitable structural intermediate between the two families, but he rejected *Elpidophorus* as an ancestor of *Planetetherium* on the grounds that they were approximate contemporaries. This objection is no longer valid, however, for the range of *Elpidophorus* has since been extended back at least into Torrejonian time. Szalay (1969) reviewed the status of relationships between the Plagiomenidae and the Mixodectidae and concluded that available evidence does not support such ties. Nevertheless, the cheek teeth (both upper and lower) of *Elpidophorus* are quite similar to those of *Plagiomene*, sufficiently close to suggest that more than convergence may be involved. It is possible that *Elpidophorus* lies in or near the ancestry of the Plagiomenidae (cf. Sloan, 1969: fig. 6).

The Picrodontidae were placed in the Dermoptera by Romer (1966), but I concur with Szalay (1968: 32) that there is no evidence to support this.

If the Plagiomenidae are truly related to the living flying lemurs, as seems probable on the basis of dental evidence pre-

sented above and by Matthew (1918) and Szalay (1969), the Dermoptera have been distinct from other mammalian groups since at least Late Paleocene time. Recent dermopterans have acquired a peculiar suite of specializations (including in particular the dental specializations and the patagium) which is not found in other mammals. In view of these considerations, recognition of ordinal status for the Dermoptera (as accepted by Simpson, 1945; Grassé, 1955; Butler, 1956; Walker, 1964; Anderson and Jones, 1967; among others) seems fully warranted.

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Donald E. Savage kindly sent me a copy of a manuscript (Russell, Louis, and Savage, in press) describing a new form from the Eocene of France. Casts of the new specimens were generously provided by D. E. Russell. I am grateful to Russell, Louis, and Savage for graciously permitting me to include herein a dissenting view on the allocation of this new species.

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